

Research Article

Evidence for Use of *Alliaria petiolata* in North America by the European Cabbage White Butterfly, *Pieris rapae*

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Pieris rapae L., an invasive crop pest, may have recently begun using *Alliaria petiolata* Bieb. (Cavara & Grande), a European invasive biennial. We investigated how *P. rapae* uses forest habitats for nectar and oviposition and examined larval performance on *A. petiolata* in the field and laboratory. Being known primarily to occupy open habitats, we found that *P. rapae* regularly uses forest edge habitats, most surveyed *A. petiolata* plants had *P. rapae* damage, and *P. rapae* successfully used both stages of *A. petiolata* for larval development.

1. Introduction

Although some of the 50,000 alien species introduced into the United States have economic value, organisms unintentionally introduced to novel habitats have been estimated to cost the United States almost \$120 billion in agricultural and economic damages each year [1]. Invasive species also cause untold damages to natural habitats through changing nutrient cycles, altering resource competition, and affecting the physical landscape structure around them, including nutrient cycling [2]. Where rare species live, invasion by novel plants or animals can cause vulnerable species to become endangered or extinct [3].

Pieris rapae L. (small cabbage white; Lepidoptera: Pieridae) is a multivoltine European butterfly accidentally introduced to Quebec, Canada, in 1860. A specialist on glucosinolate-containing Brassicaceae host plants, it soon became a destructive crop pest in North America, moving south and west as far as Kentucky in just 12 years [4]. Being now ubiquitous and abundant across the United States and Canada, it is known as a butterfly of open meadows, crop plantings, and sunny areas where its cultivated and wild hosts are typically found [5, 6].

Its primary hosts in its native range include *Armoracia rusticana*, *Brassica* spp., *Cardamine* spp., *Crambe maritima*,

Sisymbrium officinale, and *Tropaeolum majus*, among others, most of which are high light requiring plants [7]. In North America, it benefits from habitat fragmentation and disturbance favoring growth of its weedy hosts, such as *Barbarea vulgaris*, introduced *Brassica* species, and *Lepidium* species, many of which are also nonnative [8–10]. As a common pest on commercial brassicaceous crops, *P. rapae* is highly visible as an adult and more cryptic in its larval stage and has been controlled in the past through application of DDT and Bt, along with introductions of *Cotesia glomerata* and *C. rubecula* parasitoid wasps [6, 11, 12].

Although it regularly uses crop plants in North America, *P. rapae* may also use the invasive European biennial *Alliaria petiolata* Bieb. (Cavara & Grande), in part due to the plant's increasing abundance in the understory and close relationship with other host plants in the Brassicaceae. Unlike most other potential hosts, *A. petiolata* is unique in its shade-tolerance and occupancy of forest edges and understories. This invasive mustard allelopathically affects mycorrhizal forest plants as well as competes directly with neighboring plants for resources [13, 14]. Anecdotal observations suggest that this plant is much more abundant in North America than in Europe, and its presence may draw *P. rapae* into forests more often [15].

There are not many herbivores that use *A. petiolata* as a food source in North America. Although Yates and Murphy [16] identified three arthropod herbivores present on *A. petiolata* in Ontario, Canada (*Ceutorhynchus erysimi* Fabr., *Plutella xylostella* L., and *Philaenus spumarius*), they did not observe *P. rapae* consuming *A. petiolata*, and no herbivore eats enough to control its spread or abundance. Even mollusks avoid consuming *A. petiolata*, instead preferring more palatable native plants [17, 18]. This suggests that *A. petiolata* is generally well defended from most North American herbivores, and the damage that it does accrue rarely reduces plant fitness. However, *P. rapae* may be able to use the European plant as a host in North America, especially since there is some evidence of it being used as a host in Europe [7]. At present, only rare, anecdotal observations exist of the use of forested habitats by *P. rapae* in North America [19–21].

To investigate how *P. rapae* is using forested habitats and the host plant, *A. petiolata*, in North America, we directly observed *P. rapae* oviposition and nectaring behavior in forested habitats shared with *P. virginienensis*, a native congener. We also investigated how *P. rapae* uses *A. petiolata* in forest edge habitats. Finally, we compared the performance of *P. rapae* larvae and adults fed *A. petiolata* to that observed on its more typical hosts, *Brassica juncea* and *B. oleracea*.

2. Methods

2.1. Direct Observations of *P. rapae* in Forest Habitats. Observations of *P. rapae* occurred from April to June in 2011, 2012, and 2013 at three sites known to be occupied by *P. virginienensis*: a private site in Morrow Co. (MCO), OH, Wooster Memorial Park (WMP) in Wooster, OH, and Allegany State Park in Salamanca (ASP), NY. Basic visual observations were recorded using field notebooks and photography. Sites were surveyed in tandem with surveys for *P. virginienensis*, a related native butterfly. More details about observation protocols and site histories can be found in Davis and Cipollini 2014a, b publications [21, 22].

More detailed behavioral observations were made at WMP. Twenty-five *Pieris rapae* individuals were monitored between 1100 and 1600 on Apr. 15 and 18, 2012, at least 300 meters away from the nearest edge or agricultural habitat. Behaviors of individual butterflies were recorded in ten-second intervals until the butterfly left the area and included flying, gathering nectar, oviposition, and resting. Although ten seconds is longer than the time required for *P. rapae* to oviposit, we gathered enough observations to capture the rate of oviposition through time.

We identified all plants that the butterflies interacted with during oviposition and nectar gathering using the Newcomb [23] guide to wildflowers. Butterflies were identified as *P. rapae* and not as the native *P. virginienensis* by distinct, dark spots on the dorsal wing surfaces and yellow scales on the ventral wing surfaces. In contrast, *P. virginienensis* is white with occasional wing-vein shading and light spots on the wings [4].

We also observed herbivory by *P. rapae* caterpillars at WMP during the same observation periods. Although

the first instar *Pieris* caterpillars are difficult to identify to species, older *P. rapae* caterpillars develop a broken yellow line along the dorsal surface and yellow spots around the spiracles; these characters are missing in native *P. virginienensis* caterpillars [4].

2.2. Herbivory by *P. rapae* on *A. petiolata* in Edge Habitats. We examined how frequently *P. rapae* uses *A. petiolata* as a larval host plant in wooded habitats by measuring end-of-year herbivory on first-year *A. petiolata* plants in maple-beech-oak forests surrounding Dayton, OH. All herbivory experiments that follow were performed in late fall, when any *P. rapae* in the area would be in diapause as pupae. This ensured that we recorded a maximum amount of damage on individual plants.

In 2011, we surveyed approximately 9000 m² of a recreational trail in Beavercreek, OH, between Grange Hall Road and N. Fairfield Road (BCT, western corner: 39.734756N, 84.082472W; eastern corner: 39.724096N, 84.060070W). This trail has grass and unmanaged shrubs on the southern side and a strip of second-growth forest (20–60 m forest perpendicular to the trail) on the northern side. In 2013, we returned to resurvey BCT and also surveyed two other sites: Narrows Reserve in Beavercreek, OH (NAR, located at 39.691313N, 84.030293W), and Fairborn Community Park in Fairborn, OH (FCP, located at 39.789345N, 84.009446W). Approximately 3000 m² and 2400 m² were surveyed at NAR and FCP, respectively. All three sites had parking lots, recreation trails, and forest areas. We walked the perimeter of each study area and systematically examined every rosette *A. petiolata* within 3 m of the open area. In patches with more than 10 rosettes clumped together, we randomly chose 10 plants to sample. We surveyed 99 plants at BCT in 2011. In 2013, we surveyed 136 plants at BCT, 53 plants at FCP, and 81 plants at NAR.

Plants with at least one leaf larger than 5 cm in diameter (most *A. petiolata* individuals) were surveyed for chewing damage from caterpillars (asymmetrical, smooth holes away from the leaf edge) on fully expanded leaves. Our observations of *P. rapae* damage are indirect only because the surveys were performed after *P. rapae* caterpillars had pupated for the winter. Damage was attributed primarily to *P. rapae* caterpillars for several reasons. First, caterpillar damage is distinct from other causes of damage and disease, including deer herbivory, slug herbivory, and flea beetle damage (SLD and DC, personal observations). Second, we have observed *P. rapae* caterpillars feeding on *A. petiolata* throughout the year at these locations, and *P. rapae* is the only caterpillar that we have ever observed feeding in this area, despite reports of *Plutella xylostella* as another lepidopteran herbivore on *A. petiolata* [16]. Finally, several other researchers have confirmed these observations of *P. rapae* feeding on *A. petiolata* in both Ohio and Massachusetts (John Stireman and Frances Chew, personal communications). Although some leaf tearing and disease were noted (especially the presence of a powdery mildew fungus [24]), these observations were excluded from analysis of herbivory. Each leaf on a chosen plant was scored for leaf area loss by caterpillars from 0 to 5

(undamaged, 1–20%, 21–40%, 41–60%, 61–80%, and 81–100% leaf loss). The damage rating was converted to percent leaf loss by weighing each leaf score as follows: 0 (0), 1 (0.1), 2 (0.3), 3 (0.5), 4 (0.7), and 5 (0.9). The leaf scores for each plant were averaged into a final plant score. We used the indices 1–5 because precise measurements of leaf damage in the field were not possible.

2.3. *Pieris rapae* Larval Performance Assay. In order to determine the suitability of *A. petiolata* as a larval host, we examined *P. rapae* larval performance on both rosette and flowering *A. petiolata* (Wright State Forest, Dayton, OH) and on two commercial brassicaceous crops, *B. juncea* and *B. oleracea* (Meijer, Inc.). *Pieris rapae* eggs (Carolina Biological Supply) were raised on either *Brassica oleracea* L. “green cabbage” (Meijer, Inc.) or flowering *A. petiolata* and allowed to emerge as adult butterflies. We used second generation butterflies because field grown rosette *A. petiolata* (used below) was too small to be useful when the shipment of eggs arrived. Between ten and fifteen adults were placed in 75 L aquaria with artificial nectar (20% sucrose : water solution on delicate task wipes until moist) and allowed to oviposit on flowering *A. petiolata*. Eggs laid by the adult butterflies were used in the following larval performance experiment. We distributed eighty neonates evenly among the four treatments below ($n = 20$ per treatment).

After hatching, second generation neonates were placed on either field-collected (June 2014) rosette *Alliaria petiolata*, flowering *A. petiolata*, commercially purchased, nonorganic *B. oleracea* (green cabbage, Meijer, Inc.), or *B. juncea* (southern giant curled mustard, Meijer, Inc.) leaves in moist filter-paper lined Petri dishes and kept in a 16 : 8 L : D incubator at room 25 deg. C. Caterpillars were kept individually to mimic the solitary nature of *P. rapae* caterpillars in the wild. Commercial plants were rinsed with distilled water before use. We chose *B. oleracea* and *B. juncea* to represent commercial hosts available to *P. rapae* in the wild. Caterpillar habitats were cleaned daily and stocked with an overabundance of host plant material to prevent starvation or time without eating. After one week of monitoring daily for survival, we took daily measurements of caterpillar mass, until they neared pupation. Pupae were weighed and placed in 75 L aquaria according to their larval host plant, with artificial nectar and an oviposition substrate (rosette *A. petiolata*). After eclosion, butterflies were allowed to mate and oviposit freely. When all butterflies died, the number of eggs and the number of females were counted to calculate the mean number of eggs laid per female, an indirect measure of fitness.

2.4. Statistical Analysis. All statistical analyses were performed in *R* [25]. We separated our field herbivory data into two sets: data from BCT alone and data from 2013 alone. These data were separated because only one site, BCT, was sampled for two years. For both datasets, we used a binomial model with a logit link function followed by Tukey’s HSD test (multcomp package) to examine how the number of leaves on a plant covaried with location (2013 data, predictor) or year (BCT data, predictor) to affect the presence or absence of

damaged leaves (response variable) [26]. We also examined the same datasets (2013 and BCT data) for differences in the percent leaf loss score. We removed all zeroes because we were only interested in damaged plants, log-transformed the percent leaf loss scores to meet normality assumptions, and then evaluated the data using a generalized linear model followed by Tukey’s HSD post hoc testing when appropriate. Plots were constructed with the gplots package [27].

For the larval performance experiments, we used the Kaplan-Meier estimator for survival data (survival package) and one-way ANOVA to compare pupal mass and relative growth rate across host plants [28]. Relative growth rate (RGR) was calculated as larval mass increase (from day 7 until pupation) divided by the initial larval mass times the number of days of recorded growth. Chi-square testing followed by chi-square tests with Bonferroni correction was used to evaluate differences between the number of eggs laid per treatment.

3. Results

3.1. Direct Observations of *P. rapae* in Forest Habitats. At MCO and ASP, we regularly observed *P. rapae* flying in heavily wooded areas but did not observe any nectar gathering or oviposition behavior. We found an unidentified first instar caterpillar in 2012 at MCO on *A. petiolata* that could have been either *P. rapae* or *P. virginensis*. At WMP, we observed *P. rapae* adults gathering nectar in the understory from several plant species, including *Claytonia*, *Phlox*, and *Viola* species, as well as from *A. petiolata* itself. We also observed 3 female *P. rapae* ovipositing on *Cardamine diphylla* and photographed an older *P. rapae* caterpillar feeding on *A. petiolata* (Figure 1). Additionally, *P. rapae* caterpillars have been observed feeding on *A. petiolata* outside of the Wright State University greenhouse (2012–1015), on *A. petiolata* in the Wright State University woods, and in residential and park areas in Fairborn and Beavercreek, OH (SLD, personal observations).

3.2. Herbivory by *P. rapae* on *A. petiolata* in Edge Habitats. Although overall percent leaf loss was low, 78.8% of plants were damaged by caterpillars in 2013, indicating that *P. rapae* commonly uses *A. petiolata* in North America. In 2013, both the number of leaves ($z = 3.475$, $P < 0.01$) and the location ($P < 0.01$) influenced the probability of plants being attacked. BCT was significantly different from NAR ($z = 2.614$, $P < 0.05$) and FCP ($z = 3.631$, $P < 0.01$), but the latter two were not significantly different from each other ($z = -2.217$, $P > 0.05$). Across years at BCT, only the number of leaves was a significant factor in the model ($z = 3.622$, $P < 0.01$), indicating no difference in plant damage between years. Evaluating the percent leaf loss score revealed similar results, with BCT being significantly different from both NAR ($z = 2.387$, $P < 0.05$) and FCP ($z = 3.697$, $P < 0.01$), but NAR and FCP were not significantly different from each other, and the number of leaves per plant was not correlated with the percent leaf loss score. The model evaluating percent

TABLE 1: Mean percent survival, days to pupation, pupal weight, and relative growth rate with standard error of *P. rapae* (both sexes) between four host plants ($n = 16$ per treatment). Different letters indicate significant differences ($P < 0.05$).

Treatment	Survival (%)	Days To pupation (d)	Pupal mass (g)	Relative growth rate ($\text{g g}^{-1} \text{d}^{-1}$)
<i>A. petiolata</i> rosette	56.25	15.33 ± 0.85	0.128 ± 0.003	$0.277 \pm 0.046^{\text{ab}}$
<i>A. petiolata</i> flowering	20.00	15.33 ± 1.45	0.112 ± 0.008	$0.182 \pm 0.031^{\text{b}}$
<i>B. oleracea</i> “cabbage”	68.75	16.63 ± 0.28	0.134 ± 0.004	$0.294 \pm 0.019^{\text{ab}}$
<i>B. juncea</i> “mustard”	56.25	12.78 ± 0.46	0.132 ± 0.006	$0.380 \pm 0.044^{\text{a}}$



FIGURE 1: Mature *P. rapae* caterpillar consuming rosette *A. petiolata* in Wooster, OH. Photo taken on May 11, 2012, by SLD.

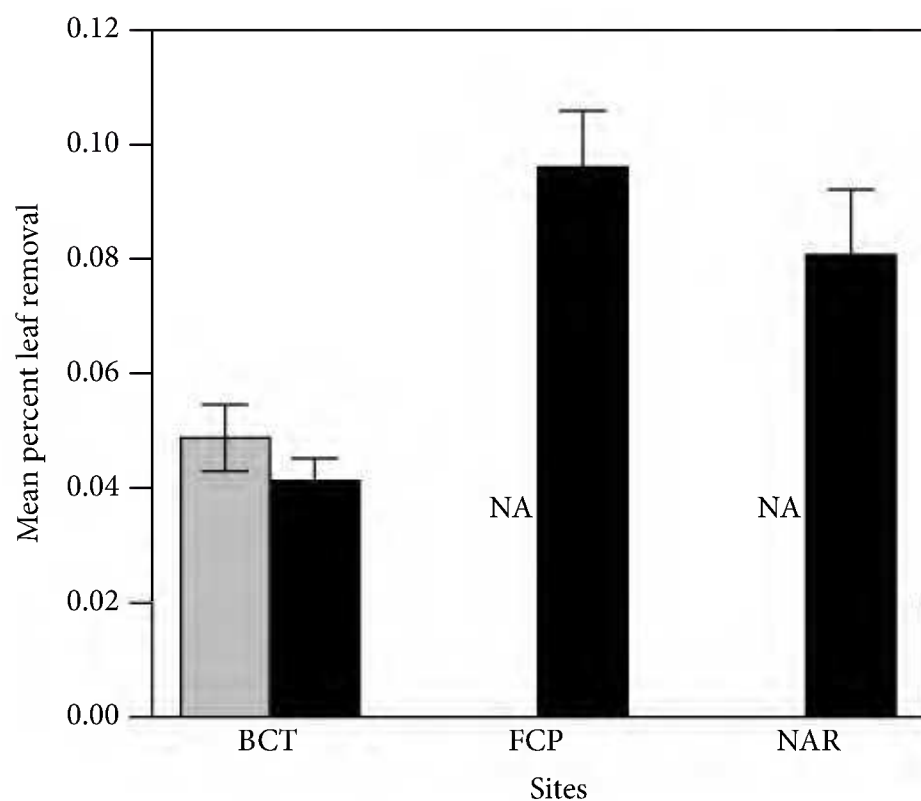


FIGURE 2: Herbivory (percent leaf loss) on *A. petiolata* varied between sites and habitats in 2013. Gray bar represents data from 2011; black bars represent data from 2013.

leaf loss score as influenced by date and number of leaves for the BCT site alone was not significant. Figure 2 shows the mean percent leaf loss score for both sites and years.

3.3. *Pieris rapae* Larval Performance. Although there was a trend towards lower survival of *P. rapae* caterpillars feeding on flowering *A. petiolata*, we found no significant differences in survival of *P. rapae* caterpillars on the four hosts that we tested ($\chi^2 = 7.4$, $df = 3$, and $P = 0.0596$, Figure 3).

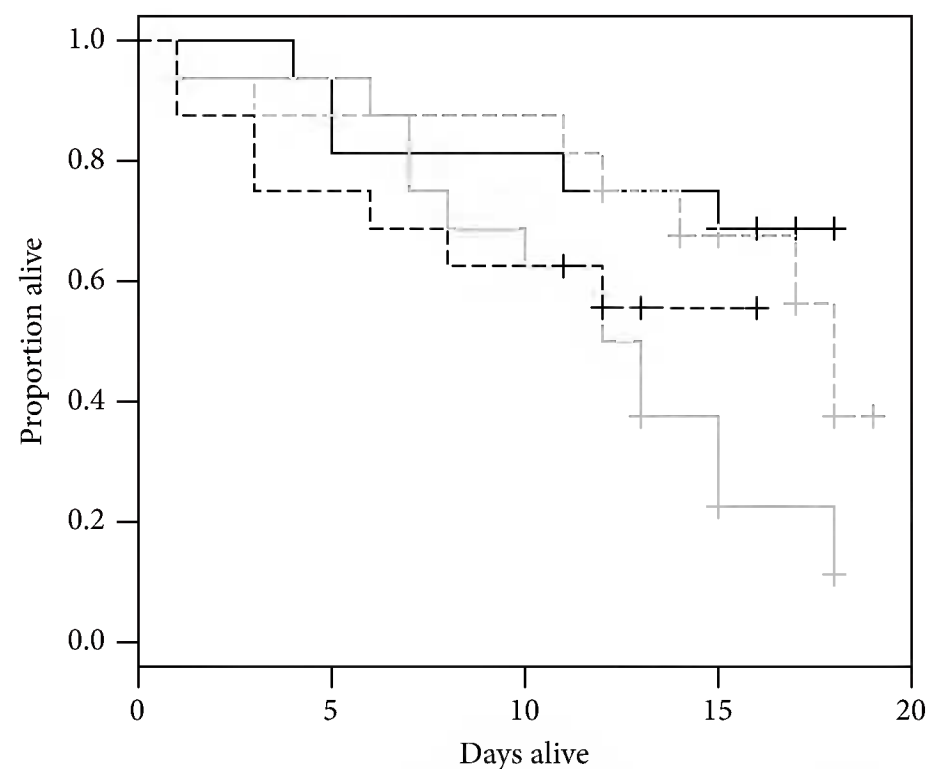


FIGURE 3: Kaplan-Meier survival estimates of *P. rapae* caterpillars fed commercial cabbage (solid black), rosette *A. petiolata* (dash grey), flowering *A. petiolata* (solid grey), or commercial mustard greens (dash black).

Pupal mass did not vary between treatments ($F = 2.213$, $df = 3$, and $P = 0.109$); however, there were differences in time to pupation ($F = 7.897$, $df = 3$, and $P < 0.01$). Caterpillars reared on *B. juncea* pupated significantly earlier than those raised on rosette *A. petiolata* ($P < 0.05$, Tukey’s HSD) and on commercial *B. oleracea* ($P < 0.01$). Relative growth rates also differed between treatments ($F = 4.428$, $df = 3$, and $P < 0.01$) because caterpillars on leaves of *B. juncea* grew significantly faster than those on flowering *A. petiolata* ($P < 0.01$, Tukey’s HSD). To summarize, *P. rapae* caterpillars reared on *B. juncea* grew faster and pupated earlier with no significant loss of pupal mass, whereas caterpillars reared on flowering *A. petiolata* took longer and grew slower than those on *B. juncea*. Means and standard error of each treatment are found in Table 1.

Eclosed butterflies from the larval performance experiment were allowed to freely mate and lay eggs on rosette *A. petiolata*. Butterflies raised on *B. juncea* laid 89.5 eggs per female ($n = 4$ females, 3 males), those raised on *B. oleracea* laid 176.6 eggs per female ($n = 3$ females, 3 males), those raised on rosette *A. petiolata* laid 119.5 eggs per female ($n = 2$ females, 4 males), and the lone female raised on flowering *A. petiolata* laid 147 eggs ($n = 1$ female, 1 male). A chi-square test for proportions revealed significant differences from the mean of 133 eggs per female ($\chi^2 = 31.3284$, $df = 3$, and $P <$

0.01). Post hoc testing showed that females laid significantly fewer eggs when raised on *B. juncea* than any of the other groups, and females raised on *B. oleracea* laid significantly more eggs than either *B. juncea* or rosette *A. petiolata* raised butterflies.

4. Discussion

We looked for evidence of the nonnative butterfly, *Pieris rapae*, using *A. petiolata* in both forest and edge habitats in North America, and also examined larval performance. Previous authors have observed occasional forest use by *P. rapae* [19–21], but we demonstrate that *P. rapae* frequents forested habitats, using both native and nonnative nectar and host plants. We also confirmed that *P. rapae* successfully uses *A. petiolata* as well as its more typical brassicaceous hosts in North America. In forests shared with *P. virginensis*, *P. rapae* uses the same nectar and oviposition resources as *P. virginensis*, with one exception: *P. rapae* can successfully use *A. petiolata* as a larval host, but the native congener cannot [22, 29, 30].

One possible implication regarding the use of forested habitats by *P. rapae* is direct competition for oviposition sites (and, therefore, larval food resources) by native *Pieris* species. If *P. rapae* prefers to oviposit on the primary native host of *P. virginensis*, *Cardamine diphylla*, the caterpillars may occasionally compete for food. This competition could be limiting near pupation when native ephemeral plant hosts are in decline [31]. However, habitat sharing may benefit *P. virginensis* if *P. virginensis* practices egg avoidance like other congeners. If *P. rapae* prefers ovipositing on *A. petiolata* instead of on the native *C. diphylla*, *P. virginensis* may not lay its eggs on already occupied *A. petiolata* leaves.

The presence of *P. rapae* in forests may negatively affect adult native pierids only if nectar is a limiting resource. Nectar resources drive Lepidopteran habitat selection and fuel successful egg maturation and oviposition [32–34]. In some cases, Lepidoptera compete directly for nectar resources, attempting to dislodge other butterflies occupying desirable flowers [35]. The initial invasion of *P. rapae* may have caused a severe decline in the abundance of another native butterfly, *P. oleracea*, before the invasion of *A. petiolata* [4], though more recent authors disagree [20]. Further work needs to be done to determine if nectar availability would be limiting for native pierids persisting in forest habitats, and whether competition for nectar with *P. rapae* is important.

In North America, *A. petiolata* is an ideal host for *P. rapae*, providing nectar each spring, as well as plant material year round (rosettes persist through winter before flowering in the spring) for larval development. Although *P. rapae* may reduce the fitness of *A. petiolata* through folivore, any fitness reduction will not be substantial. Evans and Landis [36] found that the minor foliar damage recorded in field observations of *A. petiolata* actually increased fecundity of *A. petiolata*, much like grazing can positively affect grasses.

Further work needs to examine how *P. rapae* and *A. petiolata* affect each other's fitness and abundance.

In addition to its use as a larval host, the nectar resources offered by *A. petiolata* may draw more *P. rapae* to agricultural fields near forested areas and edges occupied by *A. petiolata*. Zhao et al. [37] found that *P. rapae* were more abundant in broccoli interplanted with nectar-producing plants than in broccoli monocultures. Future experiments should include an examination of *P. rapae* populations in fields with and without nearby woodlands invaded by *A. petiolata*.

There may be an increase in apparent competition for enemy-free space when *P. rapae* use forest resources in habitats already occupied by native *Pieris* species. Benson et al. [6] found no evidence that *Cotesia glomerata* L. or *C. rubecula* would attack *P. virginensis* sentinel caterpillars near meadows; however, lab work demonstrates no preferences by these wasps for different *Pieris* spp. caterpillars as potential hosts. Despite being not currently a problem, *Cotesia* may be a problem for future generations of *P. virginensis*, *P. oleracea*, and other native pierid butterflies if they begin to follow *P. rapae* into nearby forests.

Finally, *P. rapae* may interfere with volunteer-driven conservation efforts for the native *Pieris* species. There are many organizations that track *P. virginensis* populations over time, but some volunteers estimate unusually high densities of *P. virginensis* (C. Lehn, unpublished data). Some of these observations may be of *P. rapae* utilizing forest habitat for its nectar and oviposition resources. Differentiating between these Pierids at a distance, by sight or behavior, is difficult [20, 31]. Volunteers may be overestimating population sizes by misidentifying *P. rapae* as native *Pieris* spp. and consequently missing instances where populations are in decline or extinct.

In conclusion, *P. rapae* is present in North American forest habitats with and without cooccurring native pierid species, and its use of *A. petiolata* appears to facilitate its occupancy. *Pieris rapae* may be simultaneously escaping pressure from competition and parasitism, as well as increasing herbivorous pressure on the exotic mustard *A. petiolata*. Where *P. rapae* overlaps with native Pierids, there are opportunities for competition. However, more work needs to be done to investigate both the cause of *P. rapae* habitat expansion and the ecological implications of moving into forested habitat.

Conflict of Interests

The authors have no affiliations or involvement with any organization that has a financial interest in the results discussed in this paper.

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